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LIZARDS OF THE *SCELOPORUS ORCUTTI* COMPLEX OF THE CAPE REGION OF BAJA CALIFORNIA

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ABSTRACT. *Sceloporus orcutti licki* as hitherto defined is shown to embrace two cryptic species, neither of which is subspecific in relation to the allopatric *S. orcutti*: an arboreal species, *S. licki*, and a petricole, *S. hunsakeri* sp.n., from 3 mi. E of San Bartolo (holotype MVZ 73,570); both are restricted to the Cape region of Baja California. All three species, *S. orcutti*, *S. licki* and *S. hunsakeri* have identical $2n = 34$ (XY ♂) karyotype patterns, but differ in numerous other respects. In these three species, the most succinctly diagnostic character states are: presence of a dorsolateral light stripe in *S. licki* only, 59 or fewer dorsal scales plus femoral pores in most (96% of 27) *S. orcutti*, and 61 or more in most *S. hunsakeri* (98% of 61).

INTRODUCTION

Field work in 1969 indicated that the Cape Region of Baja California (the area south of the Isthmus of La Paz) is inhabited by three distinct species of *Sceloporus* which are broadly sympatric and frequently syntopic with one another (Figs. 1, 2). Two of the three species, *Sceloporus licki* Van Denburgh and a species we describe here, are sufficiently similar to one another and to *S. orcutti* Stejneger that Smith (1939) considered them variants of a single race, *S. orcutti licki*. However, Hall's discovery in 1969 that the *licki* variant was arboreal and the other petricolous prompted reexamination of material from Baja California Sur. Specimens of the unnamed taxon have been available in museums since 1890.

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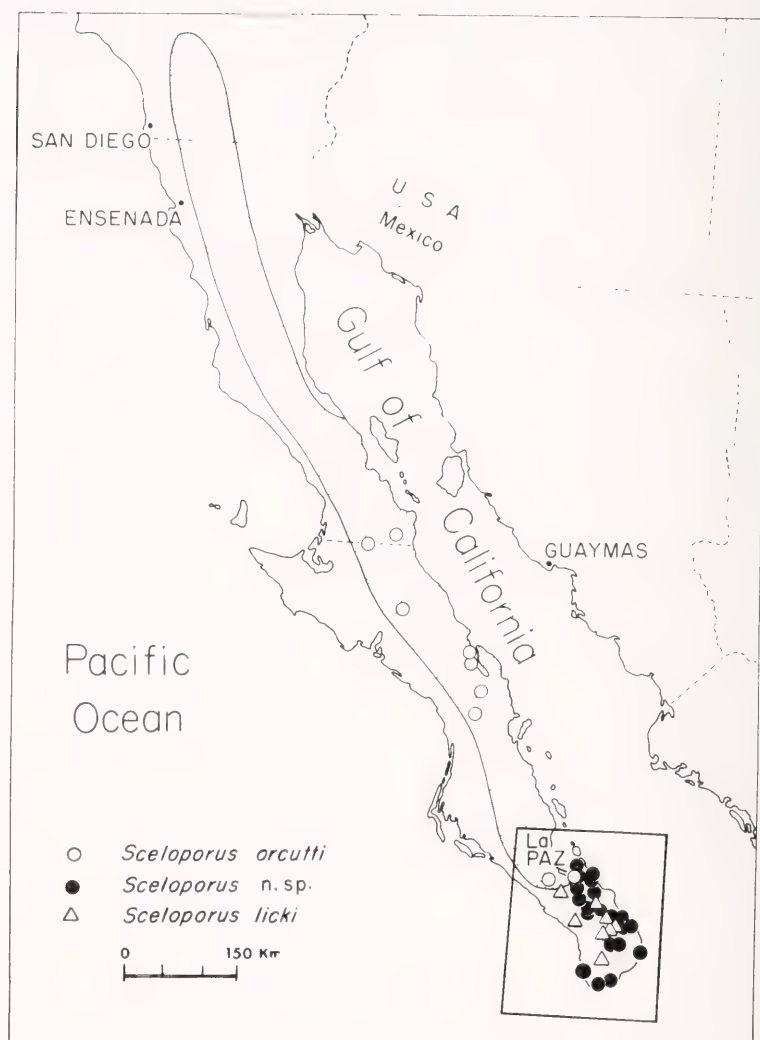


Fig. 1. Distribution of the three species of the *Sceloporus orcutti* complex in Baja California.



Fig. 2. Distribution of *Sceloporus hunsakeri*, *licki* and *orcutti* on or near the Cape region of Baja California.

Comparative material relevant to this problem has been examined from most of the major museums in the country. We are indebted to the curators and directors of these institutions. Cited specimens are referenced to collections by the following acronyms: CAS, California Academy of Sciences; CUM, University of Colorado Museum; LACM, Los Angeles County Museum; LMK, L. M. Klauber pers. coll.; LSJU, Leland Stanford Jr. Univ.; MCZ, Museum of Comparative Zoology, Harvard University; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; SDSNH, San Diego Society of Natural History Museum; UMMZ, University of Michigan Museum of Zoology; and USNM, U. S. National Museum of Natural History.

We name the newly recognized species for Dr. Don Hunsaker II, in recognition of his pioneering studies in the comparative ethology of the genus *Sceloporus* and for stimulating karyological study of its species by Hall.

Sceloporus hunsakeri, new species

Holotype: MVZ 73,570, adult male, tail complete, intact although fractured in two places in distal half, not regenerated, from 3 mi. E of San Bartolo ± 500 ft., Feb. 17, 1960, R. G. Crippen, field no. 277.

Paratypes: Thirty-three, including eight topotypes, two of which were taken on the same date as the holotype (MVZ 73,572, 73,575) and six on March 14, 1960 (MVZ 73,579-84); two from 5 mi. SW of San José del Cabo, July 6, 1970, Richard L. Holland (CUM 45,880-1); two from Migriño, 33 mi. SSE of Todos Santos, July 5, 1969, RLH (CUM 40,779-80); one from $\frac{1}{2}$ mi. N of Migriño, July 8, 1970, RLH (CUM 45,882); one from $1\frac{1}{2}$ mi. N of Migriño, July 9, 1970, RLH (CUM 45,883); two from 7 km WNW of Buenavista, 100 m, Aug. 3, 1969, W. P. Hall (MCZ R1,222,413); one from bridge at Km 105.32 on Mex. Hwy. 1, Aug. 3, 1969, W. P. Hall (MCZ R122,242); one from Cabo San Lucas, Aug. 4, 1919, J. R. Slevin (MCZ 15,565); one from 2 mi. NW of Cabo San Lucas, P. Elias, M. Merrill, and J. Lazell, Jan. 29, 1972 (MCZ R131,704); one from Cabo San Lucas, Elias, Merrill and Lazell, Jan. 29, 1972 (MCZ R131,706); 10 from 6.4 mi. E of San Lucas, Playa Pública, T. Paul Maslin, Apr. 8, 1974 (CUM 51,401-10); and three from 6.5 mi. E of San Lucas, 300 ft., T. Paul Maslin, Apr. 9, 1974 (data from last 13 not included in tabulations herein). All of the type material is from

the Cape Region south and east of the Isthmus of La Paz in the territory of Baja California Sur, Mexico.

Other specimens examined. A total of 67, all from the Cape Region of Baja California Sur, Mexico, was examined only by Hall: Agua Caliente, 800 ft. (CAS 46,790-1, MVZ 11,709-11); 2.7 mi. W of Agua Caliente, El Chorro (LACM 18,880-2); Rancho Buena Vista (LACM 18,883); 4 mi. SE of Rancho Buena Vista, Cerro Agua Amargo, 23° 36' N, 109° 37' W (MVZ 50,070); Boca de la Sierra (CAS 91,457, LACM 18,879, SDSNH 30,188-9); Cabo San Lucas (CAS 16,532-3, 46,800-6, 46,808, SDSNH 32,903); 0.3 mi. SW of Cabo San Lucas (CAS 91,446); 7.7 mi. NE of Cabo San Lucas (CAS 91,319-20); El Triunfo (CAS 46,779, 46,823, 46,826-8); 1.3 mi. N of El Triunfo (CAS 91,476); La Paz (CAS 46,775, SDSNH 17,696-8); 10 mi S of La Paz (SDSNH 30,191-3); 12.4 mi. E of La Paz on road to Las Cruces (CAS 91,255); 12.9 mi. E of La Paz, Arroyo de los Pozos (CAS 91,367); 16 mi. E of La Paz (SDSNH 30,186); 19 mi. N of La Paz [N of Pichilinke Bay] (CAS 91,093); 19.5 mi. SE of La Paz, on road to Los Planes (CAS 91,105-6); 20 air mi. SE of La Paz, 1 mi. SW of La Trinchera (CAS 91,974-6); 21 mi. ESE of La Paz, 18.5 mi. from jct. road to Los Planes and La Paz airport road (CAS 91,222); Los Frailes (SDSNH 32,920); Bahia Los Frailes (CAS 15,739); 7 mi WNW of Los Planes near Lat. 24° (MVZ 73,587-8); Ojos Negros (USNM 37,675-6; San Antonio (CAS 46,830); San Bartolo (CAS 46,787, SDSNH 38,075); 1.1 mi. SE of San Bartolo (CAS 91,384-6); 3 mi. E of San Bartolo (CAS 90,972-5); 15 mi. S of San Bartolo (SDSNH 52,991). An additional 12, all young, were examined by both authors: seven topotypes, five of which were taken on the same date as the holotype (MVZ 73,571, 73,573-4, 73,576, and 73,578) and two on March 14, 1960 (MVZ 73,585-6); one from 2 mi. NW of Cabo San Lucas, Elias, Merrill and Lazell, Jan. 29, 1972 (MCZ R131,703); one from Cabo San Lucas, Elias, Merrill and Lazell, Jan. 29, 1972 (MCZ 131,705); and three from Boca de la Sierra, 2 mi. N of Miraflores, April 17, 1977, R. Seib (MVZ 144,800-2).

Diagnosis. A small (to 86 mm ♂, 71 ♀) member of the *spinosus* group of *Sceloporus* (as of Smith, 1939; Smith and Taylor, 1950), with supraoculars in a single row (undivided) rear two in contact with median head scales, no dorsal nuchal collar, dorsal scales 33-37 (\bar{X} 35.1); femoral pores 12-18 (15.9); posterior supraocular usually (94%) in contact at least narrowly with a superciliary scale;

zero to 6 (1.9) supernumerary granules between supraoculars and superciliaries (i.e., granules in excess of a single row or parts thereof); internasals two only, rarely varying in number or position; subnasal usually (65.2%) present; preocular usually (72.3%) horizontally divided; scales between postparietals often (45.5%) four or five; number of single scales between subocular and supralabials often (64.6%) 2-4; preanal escutcheon scales 7-19; no evidence of continuous light lateral stripe in shoulder region; dark bars on throat of females and young usually not including a pair of central parallel lines; a central dark blue patch on throat in adult males; black patch on shoulder never containing a central light spot. The species is a petricole and has a $2n = 34$ karyotype.

Description of holotype. Four symmetrical postrostrals, laterals about $1\frac{1}{2}$ times as large as medial, squarish pair; a single lorilabial row contacting rostral between postrostrals and supralabials; no subnasal; two canthals; a large loreal separating 2nd canthal from lorilabials; latter in two rows posterior to middle of 1st canthal, except for interruption by one or two scales between rear of subocular and supralabials; latter 4 4 to below middle of eye; preocular divided; one enlarged, strongly keeled postocular in contact with subocular, upper postocular apparently destroyed by abrasion, others small, similar to temporals.

Two large, symmetrical internasals narrowly contacting 1st canthal, broadly contacting median pair of postrostrals and all three frontonasals; one small supranasal; two minute postnasals; median frontonasal somewhat larger than lateral frontonasals; two prefrontals, each intermediate in size between lateral and medial frontonasals, broadly in contact medially; frontal divided, posterior section $2/3$ size of anterior, narrowly contacting interparietal; one large frontoparietal on each side, $1/2$ - $2/3$ size of posterior section of frontal; interparietal large, about as broad as long, widest posteriorly; a large parietal on each side, each about $3/5$ size of interparietal; a well defined postparietal on each side, each over twice as wide as long, separated medially by 4 scales, narrowly contacting interparietal on one side only.

Supraoculars 5-5, undivided, anterior three separated from median head scales by a single row of small scales contacting posterior canthal, posterior two broadly in contact with parietal and inter-

parietal; four strongly imbricate superciliaries as seen from above, two more subimposed under junction of 3rd and 4th dorsal superciliaries; one row of small scales extending from rear edge of 1st superciliary (or very near it) posteriorly between all supraoculars and superciliaries except at posterior extremity, where 5th supraocular directly contacts (for about 3/5 of its length) rear superciliary; 2-2 small supernumerary scales (over and above one continuous row) in the area between supraoculars and superciliaries.

Auricular lobules 4-4 directly over ear opening, upper longest, next one broadest, lower one smallest and scarcely protruding over tympanum.

Infralabials 5-5 to below middle of eye; three pairs of postmentals, members of anterior pair in contact medially, those of 2nd separated by two scales, of 3rd by four; labiomenal row separating postmentals and infralabials, except for one anterior scale in each series, allowing broad contact of 1st postmental and 1st infralabial; gulars all smooth and with a single apical notch, except below ear, where a faint keel and two notches separated by a median mucrone are present on a few scales.

Dorsal scales strongly keeled, strongly mucronate, in vertebral region more acutely pointed and with fewer and shallower notches and shorter accessory mucrones than in more lateral regions, in obliquely converging rows, 33 in least count from interparietal to level of rear edge of thighs held at right angles to trunk. Ventrals smooth, with a single apical notch except at sides, where they blend with lateral scales. Femoral pores 16-17, the two series separated by six scales. Preanal scales similar to other ventrals, except for an escutcheon involving eight scales in two transverse series near posterior edge of preanal area; escutcheon scales thickened, smooth-edged, not notched, somewhat similar to femoral pore scales but the glandular (?) area spread over the entire exposed surface, not restricted to one area, and not so deeply penetrant. A deep lateral nuchal pocket, without scales; no axillary or postfemoral pocket.

Scales on limbs are smaller in general than those on body, but otherwise grossly similar; scales on rear of thighs as large as scales preceding femoral pores, but mucronate, keeled and with accessory mucrones and notches; lamellar formula for fingers 9-12-16-17-12 (9-13-16-17-12) and for toes 8-12-17-20-15 (8-12-17-20-14).

Snout-vent 78 mm; tail 117 mm; snout-posterior margin of ear opening 18 mm; maximum width of head, at ear level, 17 mm; foreleg 32 mm; hind leg 49 mm; 4th toe from base of 5th, 20.5 mm.

In preservatives, color more or less uniform dark tan above, with no markings except an iridescent bluish streak on some scales, especially along keel; foreleg with weak crossbands, more conspicuous distally; head somewhat lighter than trunk; tail with dim darker brown bands, most distinct medially.

Melanization of ventral surfaces nearly but not quite complete, with a light chin blending with a darker infralabial pigmentation crossed by a few narrow diagonal light lines; central and entire rear area of throat black with dark blue lateral highlights; black on throat extending onto anterior chest area, but light areas remaining in central lateral chest areas at level of axillae; throat color extending dorsad as a shoulder patch, light margined (one scale wide) posteriorly, entering lateral nuchal pocket anteriorly but not passing beyond it; light posterior margin crossing arm insertion; no light areas within shoulder patch. Sides of belly dark mauve, blending with a broad black median border shot with dark iridescent blue areas; lateral belly patches not fully confluent medially or with gular patch, although limited continuity exists in both areas; black in groin continuous with belly patches but rear half of ventral surfaces of thighs largely light; preanal area entirely light.

Variation. The 33 specimens in the type-series have 33-37 dorsals (33, five; 34, six; 35, five; 36, thirteen; 37, four) with a mean of 35.1. The range in the counts taken by Hall for the "other specimens" is considerably greater (range 31-41; 31, one; 33, four; 34, three; 35, nine; 36, eleven; 37, eighteen; 38, ten; 39, seven; 41, one) and the mean 36.3 is also greater. The counts by Hall were taken at various times under less controlled conditions and include several partially decornified specimens which are difficult to count accurately because the underlying scales are very soft, easily distorted and difficult to discern. Specimens reexamined by Smith with few exceptions have 1-3 fewer dorsals than Hall originally counted. Nevertheless we regard older counts that cannot now be rechecked as useful indicators of a somewhat greater range than is represented in the relatively small type-series.

The femoral pore counts taken by both authors are essentially identical and our pooled results yield a range of variation in 169

counts from 12 to 18 (12, one; 13, five; 14, sixteen; 15, thirty-five; 16, fifty-eight; 17, forty-three; 18, eleven) with a mean of 15.9. There is no significant difference between counts in the two sexes (males, $N = 98$, 13-18, \bar{X} 15.89; females $N = 58$, 12-18, \bar{X} 15.84; 13 counts not allocated to sex, 13-17, \bar{X} 15.84).

Head scale characters were recorded only for the 33 individuals of the type-series. In 66 counts on the contact of rear supraocular with a superciliary, only 4 (1.6%) had the rear supraoculars separated from the superciliaries (the first supraocular is in broad contact with the first superciliary in all). The supernumerary scales vary from 1 to 6 (0, nine; 1, seventeen; 2, twenty-one; 3, ten; 4, four; 5, three; 6, one) with a mean of 1.9.

The variation in other head scales, including very small scales, is exceptionally limited. The scales in the internasal area are especially constant relative to the variation occurring in most *Sceloporus*. All scales are as described for the holotype except: separate postrostrals four in 30, two in 1, five in 1, median pair fused with the supranasals on each side in 1, one pair of large internasals in 32, three in 1; internasals contacting anterior canthal on both sides in 21, separated by a separate small scale on both sides of two, on one side in four, by contact of a postnasal and lateral frontonasal on both sides of three, on one side in one, and in one specimen by a postnasal-lateral frontonasal contact on one side and by a separate small scale on the other. The internasals always contact the postrostrals (although the central two postrostrals are fused with the supranasals in one specimen) and frontonasals, so that always there are two scales in a straight median (or closely paramedian) line between median frontonasal and rostral. Subnasal present on both sides in 20, on one side in three, on neither side in 10; preocular horizontally divided on both sides in 21, on one side in four, on neither side in seven (indeterminate on one side in one, divided on other); postnasals 2-2 in nine, 2-3 in nine, 3-3 in 14, 4-4 in one; scales between postparietals two in two, three in 16, four in 11, five in four; postparietals contact interparietal on both sides in 29, on one side in three, on neither side in one; two enlarged, keeled postoculars in all; number of single scales contacting both subocular and supralabials 0-4 (59 counts: 0, three; 1, twenty; 2, twenty-three; 3, seventeen; 4, two); 1st canthal failing to contact lorilabials only on one side of one (lower edge split off as a separate scale); two frontoparietals on one

side in five, all others with 1-1; scales of 1st pair of chinshields separated by one scale in one, of 2nd pair by three scales in two, and by two in 31, of 3rd pair by four (14), five (18), or six (1) scales; frontal divided into three scales in one, into four in one (in the latter, the anterior of three transverse divisions is split into right and left components).

All mature males possess a clearly defined preanal escutcheon, each scale of which contains a light colored flaky tissue surrounded by a narrow border of cornified black pigmented tissue. Scales in the center of the escutcheon are more strongly modified than those towards the margin. The structure is also discernible in females and young by scale thickness and the lack of an apical notch, but the modified scales can be reliably counted only in the adult males. In 11 such individuals from the type-series, counts range from 8 to 14 (8, two; 9, two; 10, three; 11, two; 13, one; 14, one) with a mean 9.3. In 33 comparable specimens examined only by Hall, the range is 7 to 19 with a mean of 12.5 (see Comparisons for details). All counts are more or less subjective, as frequently several scales are only partially modified to various degrees.

In live, fully melanistic males (68 mm s-v and larger, as recorded in color photographs taken in the lab, within a week of capture, when the animals were at or near optimum temperature), the central gular, chest, preanal, shoulder and shank areas are black, the lateral belly patches distinctly navy blue; four to five iridescent green diagonal stripes one to two scales wide divide the blue belly patches into darker ventral chevrons, each about three scales wide. The underside of the tail is abruptly lighter than the trunk and only faintly dusky. The underside of the foreleg, chin and infralabial areas are darker, and some evidence of narrow light bars is present on the lower lips and chin. Dorsally, the basic body color is an iridescent greenish bronze to light metallic green which grades to a slaty, metallic blue or purple along middorsum from between shoulders to over the tail base. This darker area is about seven to eight scales wide at the widest and grades into the lighter ground color rather than being sharply differentiated from it. In no specimen is there a light central spot in the shoulder patch.

Adult females and subadult males are light brown to dark greenish brown or slate above, with scattered scales exhibiting an

iridescent bluish apex; lips, tail and limbs barred, more strongly on distal parts. In both sexes, 3-4 dark bars separated by lighter stripes radiate from the eye on sides of the head. A black shoulder patch is always present, light-bordered both anteriorly and posteriorly in the young. In older animals of both sexes the anterior light border becomes obscured by encroachment of black, whereas the posterior border remains intact and distinct in all specimens. Typically the upper and lower extremities of the anterior border persist for a time as isolated light spots, and in due time only the lower persists, sometimes completely enclosed by black. In mature adults even that disappears completely. In no developmental stage is there ever a central light spot within the shoulder patch. Very small individuals show about 11 transverse rows of small, obscure, dark brown spots, larger and more distinct paravertebrally, on the trunk; the series continues onto the tail. This pattern soon fades with maturity, although the row of spots at shoulder level becomes briefly accentuated and weakly collarlike, before it becomes obscured by the general darkening of the dorsal surfaces; adult females may retain vestiges of the collarlike marking but it is completely indiscernible in adult males.

On ventral surfaces, the dark gular bars are bluish, and faint bluish belly patches shading laterally to tan are visible in mature females. The medial borders of the belly patches are comparatively dark but still considerably fainter than the gular bars. The patches are separated by about five to seven scale rows along the midline.

In all young specimens the throat, chin and lower lips are whitish but prominently barred, the dark lines twice as wide as the intervening spaces and converging toward the rear center of the throat. These markings persist throughout life, except that in mature males they are extensively obscured by the black area expanding from the rear center of the throat. The throat bars seldom form parallel lines on midthroat.

One adult male *S. hunsakeri* from the paratypic series had a karyotype (MCZ Karyology catalog no. Y14,683, main catalog no. MCZ R122,241) of 34 chromosomes in the typical primitive pattern for sceloporines (Paull et al. 1976). *S. licki* and *S. orcutti* have the same chromosome number (Cole 1970, Hall 1973, in prep.). The karyotyped male *S. hunsakeri* was collected while actively involved

in territorial defense and was maintained in the lab with a female *S. hunsakeri* and several *S. licki* for seven weeks before being sacrificed for karyology. The male was frequently seen courting the female throughout this time. He paid no attention to the *S. licki* housed in the same cage. When karyotyped, his testes still showed active spermatogenesis, with high frequencies of spermatogonial mitoses, meiotic prophases, second metaphases and maturing spermatids. We conclude from this that the male was sexually active at least from the period of collection, 3 Aug. 1969, through 24 Sept., when it was karyotyped.

Ecologically, *S. hunsakeri* appears to be a strict petricole and extremely wary. Many were observed 2-3 August 1969, when Hall was collecting in the Cape region of Baja California, but except for the two male *S. hunsakeri* collected while actively displaying to one another and a female trapped under a small bridge, all took alarm at a distance many times the 2 m length of the noose pole. In most cases, just at the sight of the collector's vehicle, they escaped into deep crevices or under massive boulders. None were observed in alluvial or wooded areas lacking massive rock outcroppings. Essentially all collection localities recorded for *S. hunsakeri* are rocky.

Comparisons

Past consideration of *S. licki* as a subspecies of *S. orcutti* was a product of 1) the similarities of *S. hunsakeri* and *S. licki* in size and squamation; 2) the close parallelism of *S. hunsakeri* and *S. orcutti* in ecology and coloration; and 3) the near parapatry of *S. orcutti* and *S. hunsakeri*. To establish *S. hunsakeri* and reestablish *S. licki* as valid species we must show: 1) that the differences between *S. hunsakeri* and *S. licki* are sufficient to rule out the possibility that these are not simply different morphs of a polymorphic population (as Smith [1939] originally believed); and 2) that the differences between *S. hunsakeri* and *S. orcutti* are sufficient to indicate the probable existence of *intrinsic* barriers to gene flow between the two populations.

S. hunsakeri vs. *S. licki*. Although *licki* and *hunsakeri* are essentially identical in body and head proportions, in femoral pore and body scale counts, and in most cranial scale characters, other differences are of a degree and nature that cannot be accounted for by allelic differences at a small number of loci. Most of the

differences are summarized in Table 1. The most constant differences in scutellation pertain to the relation of the posterior supraocular to the superciliaries (Fig. 3), irregularities of internasals (Fig. 4) and the size of the escutcheon (Fig. 7). In *S. hunsakeri* the modified escutcheon scales are in two or more transverse rows, whereas in *S. licki* usually only one scale row is involved, with three to five scales fully modified and a couple more partially so (i.e., at least half of the scale surface modified). A few additional scales, not counted in the tabulated totals, may show slight modifications of the scale tip. Though in *S. hunsakeri* more scales are involved in the secretion, not all are as sharply differentiated from the surrounding normal scales. The developmental field controlling differentiation appears to have a much smoother gradient so that the scales at the anterior and lateral peripheries of the escutcheon are all only partially modified. Thus the counts of these scales for both *S. hunsakeri* and *S. orcutti*, which have similar developmental patterns for this character, are not precise. Some females and juveniles show

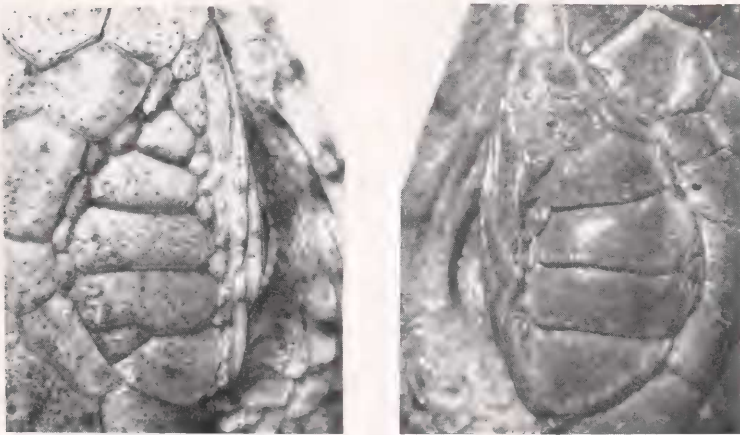


Fig. 3. Contrast between *S. licki* (left, MVZ 144,803) and *S. hunsakeri* (right, MCZ R122,241) in number of supernumerary scales between superciliaries and supraoculars, and in contact of posterior supraocular with superciliaries (actual field length is 8.6 and 9.1 mm respectively). In 144,803, rear supraocular and superciliary are completely separated by small scales and five supernumeraries. In R122,241, rear supraocular contacts rear superciliary, and two supernumeraries present.

TABLE 1. COMPARISON OF *S. HUNSAKERI*, *S. LICKI* AND *S. ORCUTTI**

<i>Character state</i>	<i>hunsakeri</i>	<i>licki</i>	<i>orcutti</i>
Snout-vent length, max.	87 mm (85)	78 mm (8)	109 mm (28)
Posterior supraocular contacting superciliary	62(66) 94%	0(16) 0%	3(20) 15%
Supernumeraries between supraoculars & superciliaries**	0 6(1.9) (33)	0 6 (3.1) (16)	
Specimens with internasal scale deviations	1 (33)	6 (8)	9 (10)
Subnasal present	43(66) 65.2%	6(16) 37.5%	18(20) 90%
Preocular divided horizontally	47(65) 72.3%	2(16) 12.5%	
Scales between postparietals	2 5(3.5) (33)	2 3(2.9) (8)	2-4(2.6) (10)
Single scales between subocular and supralabials	0 4(1.9) (65) (94.9% 1 or more)	0-2(0.8) (16)	0 1 + (23.8% 1 or more)
Scales in preanal escutcheon 65 mm + s-v ♂♂	7 19(11.7) (33)	4 7(4.6)	—
Frontoparietals separated	33(33) 100%	—	43(61) 70.5%
Adult ground color	♂ iridescent bronze-green to blue; ♀ dull, slaty dark green to brown	♂♂ rich tan to brown; ♂ overwashed bluish-purplish iridescence	diagonally cross-barred

<i>Character state</i>	<i>hunsakeri</i>	<i>licki</i>	<i>orcutti</i>
Dorsolateral stripe, light tan to cream	none	2 scales wide on neck, wider, less sharply defined toward pelvis	none
Black shoulder patch	no center spot; white rear border	white to iridescent blue center spot tan rear border	
Gular pattern	bars; rarely parallel paramedian lines; ad. ♂♂ mostly or all black-suffused	bars; often parallel paramedian lines; never black-suffused	no black suffusion
Lateral belly patches ♂♂	fused with gular patches; darkest laterally or all dark	not fused; darkest medially	not fused; no black suffusion
Habitat	petricolous, low to intermediate altitude	arboricolous, intermediate to high altitude	petricolous
Reaction	very wary	easily approached	very wary

*Parenthetic figures means and total specimens (or sides) counted.

**The small scales exceeding 1 complete row.

some degree of modification of the preanal scales but never to the extent seen in the adult males. The appearance of the escutcheon strongly suggests an organ specialized for the secretion of a substance to be rubbed against the substrate as the vent is wiped across it. Since fully developed escutcheons are only found in reproductively mature males, the secretion may have a pheromonal function possibly involved in maintaining reproductive isolation.

The scale differences between the two species, though not conspicuous, are diverse and distinctive. However, differences are strikingly apparent in color pattern and appear to be completely diagnostic in living and preserved material (Fig. 5). Color observations are based on the entire series of preserved specimens examined by Hall, on color transparencies of live specimens of both sexes and on the preserved material available to both authors. One set of

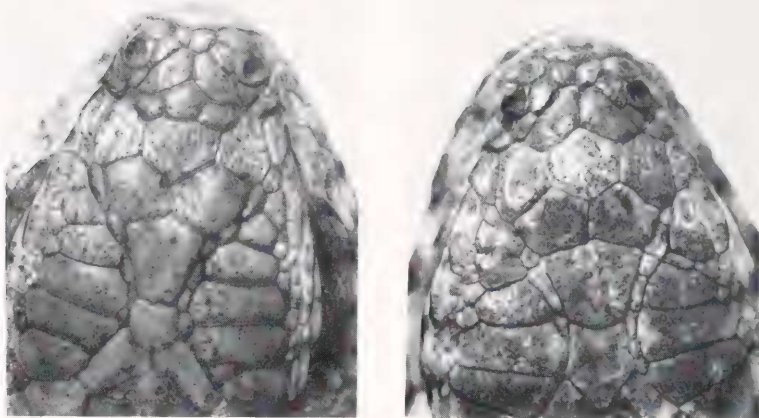


Fig. 4. Contrast between *S. licki* (left, MVZ 144,803) and *S. hunsakeri* (right, MVZ 144,800) in structure of internasal area; actual field length 11.5 mm in each (in median line). In 144,803 three posterior internasals, two primary internasals, latter separated from first canthal on each side by tiny scale posterior to an upper (left) and 2nd (right) postnasal; the four postrostrals irregular; supranasal on each side relatively large, frontoparietals in contact. In 144,800, primary internasals the only internasals present, separated from first canthal on each side by contact of upper postnasal and lateral frontonasal; this symmetry is typical.

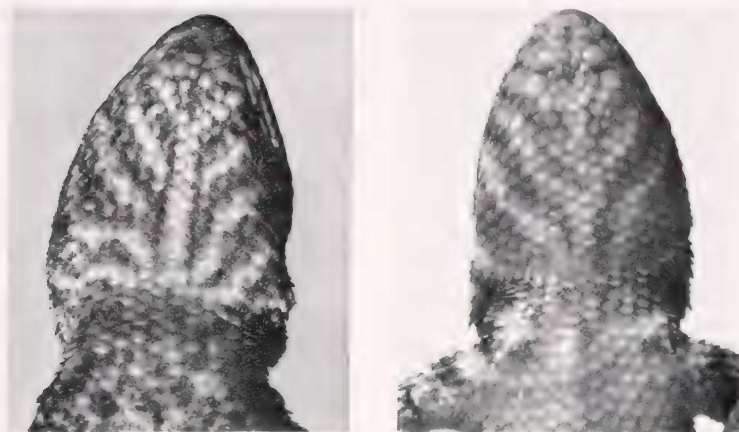


Fig. 5. Contrast between young male (39.5 mm s-v) *S. licki* (left, MVZ 73,577) and young male (35.5 mm s-v) *S. hunsakeri* (right, MCZ R131,703) in pattern of throat bars; actual field length 16.0 and 16.5 mm respectively. Parallel paramedian lines pronounced in 73,577, visible throughout life in both sexes since males lack a central rear gular patch; in R131,703 the lines are largely oblique, scarcely parallel at any point, and are obscured in adult and subadult males by a rear central gular patch.

differences associated with overall ground coloration and patterning appears to be correlated with ecological differences between the species. The remaining differences all relate to specific body areas presumably used in social signaling and species recognition.

The body color below the dorsolateral light stripe also shows some patterning of slightly lighter vertically elongated spots in both sexes of *S. licki*. In the field, differences in basic ground coloration and the conspicuously visible dorsolateral stripes of *S. licki* allow the collector to distinguish between these two species from distances of many meters. These differences are correlated with the basic colors of the preferred substrates frequented by each species. The relatively dull and uniform pattern of *S. hunsakeri* is adaptive to its habitat on unpatterned rocks, whereas the *S. licki* pattern is equally as disruptive as the light and shadow on or under the trees that constitute the habitat for that species.

Other color differences are all associated with body structures presumably involved in social signaling and/or species recognition.

The dark shoulder patch seems likely to serve as an orientation mark for lateral displays (Fig. 6). In *S. hunsakeri* it may be set off in front by a light line or series of spots in incompletely melanized individuals. Faint ventral patches are visible in females of both species, but unlike the contrast in males, they are more intense medially, with the median dark edges separated by several scale rows.

Although karyotypes of *S. hunsakeri*, *S. licki* and *S. orcutti* are identical (Cole 1970, Hall 1973, in prep.), there is evidence that the reproductive seasons of *S. licki* and *S. hunsakeri* differ. Two *licki* males were karyotyped, one six days after capture 6 August (MCZ original number Y18,801 = MCZ 136,188), the other about seven weeks after capture (MCZ original no. Y14,689 = MCZ R122,233). Both showed completely regressed testes, with the seminiferous tubules collapsed to a few mm³ within the loose and shriveled tunica, only a few mitoses and no hint of sperm or any stage of meiosis. On the other hand, the *S. hunsakeri* male karyotyped after 7 weeks of captivity still showed very active spermatogenesis and

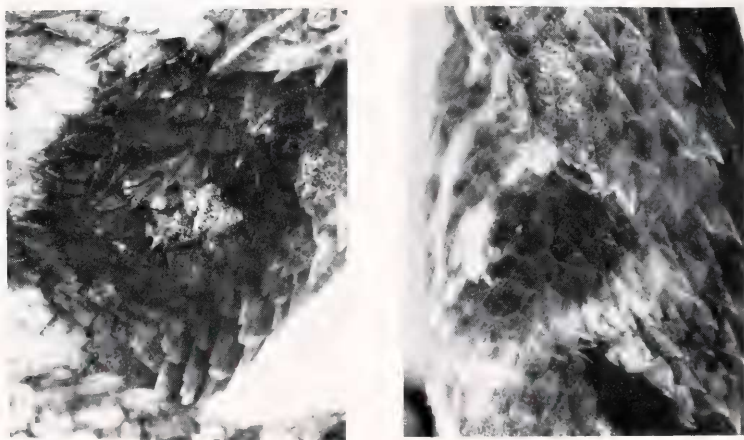
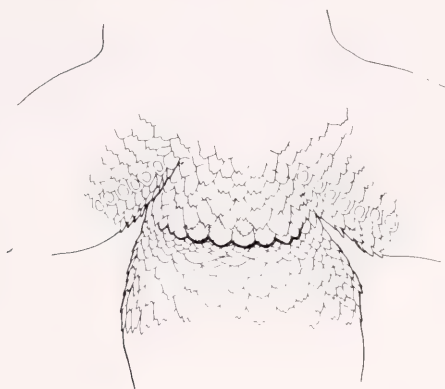


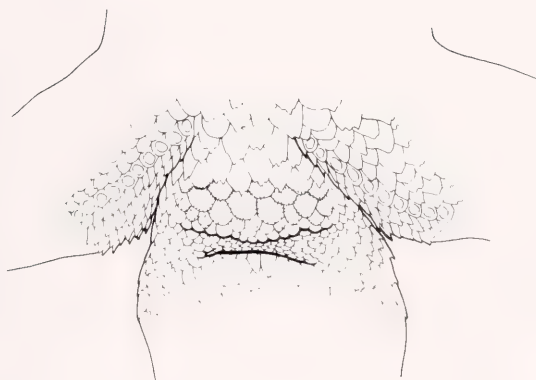
Fig. 6. Contrast between young male (39.5 mm s-v) *S. licki* (left, MCZ 144,803) and a subadult male (61.5 mm s-v) *S. hunsakeri* (right, MCZ 73,575) in relation of dark shoulder patch to a central light spot; actual field length 5.8 and 12.0 mm respectively. A light dot, conspicuous in life but small here, within dark spot in *S. licki*, absent in *S. hunsakeri*.

*Sceloporus licki*

Paratype

CAS 1423

0 5 mm

*Sceloporus* n. sp.

CAS 46828

0 5 mm

Fig. 7. Contrast between adult male *S. licki* (left, CAS 1,423) and adult male *S. hunsakeri* (right, CAS 46,829) showing development of preanal escutcheon scales. In *S. hunsakeri*, last row of preanals folded under and are not visible in illustration.

courtship behavior. The *S. licki* individuals held in the same cage with the *S. hunsakeri*, though apparently in good health, showed very little social or courtship behavior. Although this sample size is small, these observations along with the visual and pheromonal differences noted above, suggest these two species may have quite different reproductive seasons.

Therefore, although these two species are similar in most characters of proportion and squamation, they show many significant differences in other aspects of their biology, and we believe they should be considered genetically independent and ecologically differentiated sympatric species. Based only on these color pattern differences, even the oldest of the preserved specimens may be easily allocated to one or the other species.

S. hunsakeri vs. *S. orcutti*. It is evident that *S. hunsakeri* and *S. orcutti* occupy similar ecological niches characteristic of strict petricoles. They also have many aspects of coloration in common (e.g., see Smith, 1939). There is no evidence that their ranges contact, except for one *S. orcutti* and four *S. hunsakeri* with locality data of "La Paz" (which may only be a collecting headquarters). The Isthmus of La Paz is an alluvial outwash from the mountains to the south and is presumably of fairly recent origin. According to topographic maps of the area (Comisión Intersecretarial Coordinadora del Levantamiento de la Carta Geográfica de la República Mexicana, 1:500,000 scale, quadrangles 12R-VII, 12R-VIII, and 12Q-II), the maximum elevation of the divide across the Isthmus between the Pacific and Gulf slopes is less than 200 m. The depicted 200 m contour indicates that at least 20 km separates any area of the Cape over 200 m from any area of the Peninsula proper over 200 m. Except for the questionable specimens from "La Paz", there are no locality records for either *S. orcutti* or *S. hunsakeri* from this lowland. Papenfuss (person. commun.) has collected extensively in this area and he does not recall having observed "*orcutti*" or any potential *S. orcutti* habitat. Presumably *S. orcutti* and *S. hunsakeri* are dichopatric, although their ranges are close to each other (specimens with reliable localities are separated by about 40 km). In the absence of sympatry to assure that reproductive isolation exists, other criteria must be examined to determine the taxonomic status of these two isolated populations.

S. hunsakeri and *S. orcutti* differ conspicuously in morphology, unlike *S. hunsakeri* and *S. licki*. A considerable size difference and diagnostic scale characters are obvious from comparisons of Baja California Sur materials (Table 1). Northern *S. orcutti* reach an even larger size than this small sample indicates.

Head scales differ in percentages of given character states but not categorically in any character. The most constant distinction we discovered lies in complete separation of the rear supraocular from the rear superciliary in most (85%) *S. orcutti* and contact in most (94%) *S. hunsakeri*. Secondly, the internasal scales are quite irregular in number and/or position in *S. orcutti*, but are seldom unsymmetrical in *S. hunsakeri*. Thirdly, the major pair of internasals contacts the first canthals on neither side in ten *S. orcutti* and on 47 of 66 sides (71.2%) in *S. hunsakeri*. Lesser distinctions are noted in Table 1.

Finally, there is little overlap in either dorsal scale or total femoral pore counts for the two species. Dorsal scales for 28 southern peninsular *S. orcutti* examined by Hall range from 29 to 34 ($\bar{X}[\pm\text{SEM}]$ 31.77 ± 1.295) while 81 *S. hunsakeri* range from 31 to 43 (\bar{X} 38.13 ± 1.884). The hypothesis of equivalency is rejected at the .005 level using the *t* test with 32 d.f. Total femoral pore counts range from 22 to 27 (\bar{X} 23.83 ± 1.381) in 28 *S. orcutti*, whereas 84 *S. hunsakeri* range from 25 to 36 (\bar{X} 31.56 ± 2.282) with equivalency rejected at the .005 level. A discriminant function can be generated from these data (Fig. 8) for 27 *S. orcutti* and 81 *S. hunsakeri* by adding the total femoral pore number to the dorsal scale count for each individual. This function separates all but two of the individuals examined. All *S. orcutti* except one have 59 or fewer dorsal scales plus femoral pores, whereas all but one *S. hunsakeri* have 61 or more. The mean value of the discriminant for 19 *S. hunsakeri* with localities within 32 km of La Paz (i.e., the Isthmus of La Paz) is 68.23 ± 2.96 compared with 68.03 ± 2.93 for all 81 *S. hunsakeri*. The four individuals from "La Paz" range from 69 to 71 with a mean of 70.0. Two *S. orcutti*, one from "La Paz" and one from 20 mi. W of La Paz are respectively 54 and 53, at the opposite end of the range of variation in *S. orcutti* from the values (60–74) for *S. hunsakeri*.

Color differences between the two species are completely diagnostic, insofar as we can compare them. *S. hunsakeri* does not

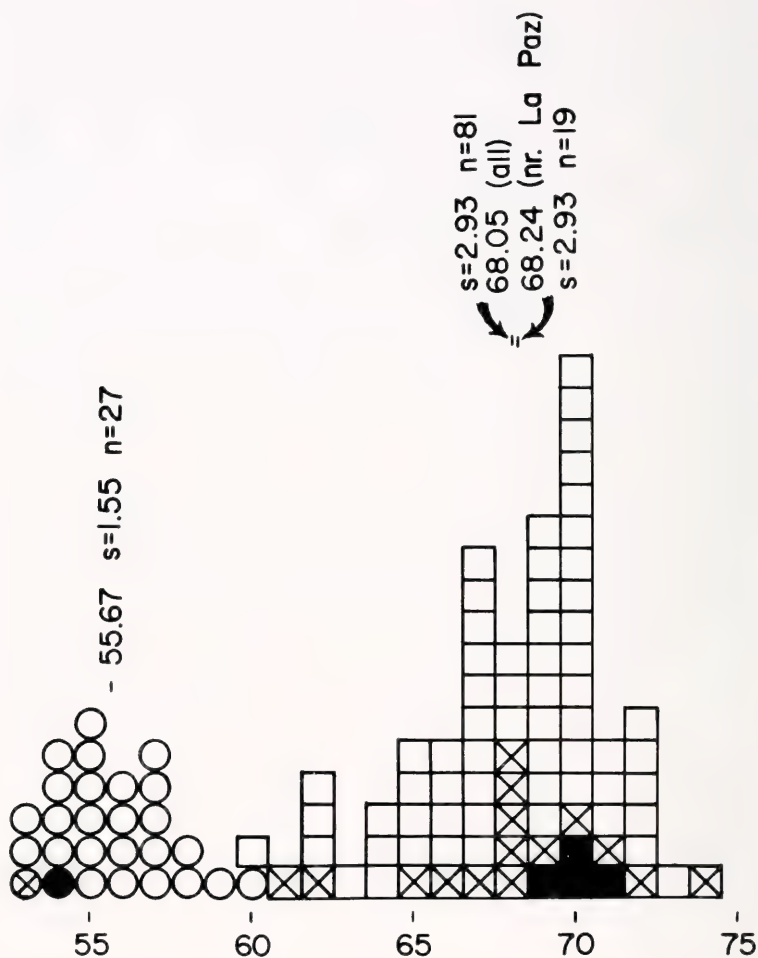


Fig. 8. Comparison of discriminant functions for *S. hunsakeri* and *S. orcutti* (most of the latter from Baja California Sur). *S. orcutti* specimens are indicated by circles, *S. hunsakeri* by squares. Solid symbols indicate specimens from "La Paz"; symbols containing an X indicate specimens with collection localities within 20 miles of La Paz.

possess the distinctive, narrow diagonal crossbars on both dorsal and ventral surfaces so conspicuous in northern *S. orcutti*. The barring, extensively obscured in adult *S. orcutti*, persists at least on the sides of the body in the largest specimens. Other differences are noted in Table 1. Southern *S. orcutti* appear to maintain these distinctions, although we do not now have substantial recent material to support this contention.

Clearly these data do not provide evidence for past or present introgression between the distinctly larger, larger-scaled *S. orcutti* and the smaller, smaller-scaled *S. hunsakeri*. To conclude this comparison we are left with the problem of assessing the taxonomic level of difference between populations which are and have been geographically separated. Our experience with the genus leads us to regard the observed differences as a strong indicator that the two taxa would be genetically isolated if they were in contact either through parapatry or sympatry, and therefore that *S. hunsakeri* should be recognized as a full species, rather than as a subspecies.

S. licki vs. *S. orcutti*. *S. licki* would never have been closely compared with *S. orcutti* if it had not been for the confusion of *S. licki* and *S. hunsakeri* from the very outset (see next paragraph), perpetuated by Smith (1939). Early workers referred or compared material representing *S. licki* to *S. undulatus consobrinus* apparently because of similarities in pattern observed also by Hall. Yarrow (1883:61) and Belding (1887:98) so identified materials taken in 1882 at "La Paz" by Belding, and Van Denburgh's (1895) primary comparison of *S. licki* was with *S. consobrinus*. That association does not now seem rational since the closest relatives of *S. licki* certainly occur in more nearly adjacent territories.

General comments on the S. orcutti complex

A single paratype of *S. licki* was recorded in Van Denburgh's description (1895:114) from San José del Cabo, taken Sept. 16, 1890, by W. E. Bryant. Given the probable lack of *S. licki* habitat there and the verified presence of *S. hunsakeri* in later collections, the Bryant specimen was probably the earliest acquisition of *S. hunsakeri*. Van Denburgh also recorded a dark central gular patch in one male of his Miraflores series (1895:112; 1922:357); that

specimen must likewise represent *S. hunsakeri*, since later collections from Miraflores confirm that both *S. hunsakeri* and *S. licki* are present in the vicinity.

Unfortunately, the California Academy of Sciences collection (including the *S. licki* type and all but three paratypes distributed to other museums) was destroyed in the San Francisco earthquake and fire. Nevertheless, Van Denburgh's type-description referred to the striped form, which he clearly differentiated from *S. orcutti* by its smaller and more sharply keeled ("rougher") dorsal scales, from *S. magister* and *S. zosteromus* by smaller and more mucronate scales, and from all of these species by color pattern. Each of the three surviving *licki* paratypes is clearly the striped morph. Two paratypes entered in the Stanford University collection at the time of the fire have since been returned to the California Academy of Science. One of these was designated by Smith (1939) as a neotype under its Stanford University tag number (neotype: CAS 1423 = LSJU 2987a; when seen by Hall, both tags were still on the specimen). The other specimen from this series is CAS 1426 = LSJU 2988. The third paratype is from the Miraflores series, and is in the U.S. National Museum of Natural History (USNM 23,749).

Stejneger (1893) described *S. orcutti* from USNM 16,330, from Milquatay Valley, San Diego County, California, collected by C. R. Orcutt. In reference to the type-locality it may be of interest to record that the bottle containing the holotype also contains a rather fragile note dated Aug. 14, 1934, signed by L. M. Klauber. We quote it here to insure against loss of the information it contains: "Orcutt once told me that the 'Milquatay' referred to was the flat just east of Campo, San Diego Co., Calif. Milquatay is said to mean wheat field in Indian, and almost any flat was known as Milquatay. The town of Guatay (or Quatay) is not the type locality of *orcutti*."

The preanal escutcheon of *S. hunsakeri* and *S. licki* discussed in the preceding account occurs in *S. orcutti* and several other species of the *S. spinosus* group as well. The development of the escutcheon in *S. orcutti* is very similar to the pattern seen in *S. hunsakeri*. However, its histology, functions, distribution in other species, and general taxonomic value remain to be explored.

Dr. George Gorman and his students at UCLA have recently begun a survey of the electrophoretic variability of the Baja California *Sceloporus*. They inform us (person. commun.) that

genetic distances between representatives of *S. orcutti*, *S. licki*, and *S. hunsakeri* are all consistent with our separation of these populations at the specific level. They also report that there appears to be electrophoretic evidence suggesting that even *S. orcutti* as we have restricted its definition may be polytypic. However, we see no supportive external morphological evidence.

Given the many taxonomic problems involved in classifying allopatric populations, we do not here make any formal attempt to allocate *S. orcutti* complex populations on the Gulf of California islands to any of the three peninsular species. This cannot be done definitively until information on the biochemical genetics of both mainland and insular populations is more complete, although external morphology and coloration will yield preliminary indications. Prior to such examination, we suggest that the Espiritu Santo and Ballena island populations may be provisionally classified with *S. hunsakeri* (although some differences in coloration are evident), and that populations from the more northern islands be grouped with *S. orcutti*.

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APPENDIX

ADDITIONAL SPECIMENS EXAMINED

(All from Baja California Sur, Mexico, unless otherwise noted.)

Sceloporus licki. *Neotype*: Sierra San Lázaro (CAS 1,423 = LSJU 2,987). *Paratypes*: Sierra San Lázaro (CAS 1,426 = LSJU 2,988); Miraflores (USNM 23,749). *Other specimens*: Boca de la Sierra (LMK-SDSNH 30,187); 2 mi. NNW of Cerro San Antonio (SDSNH 53,136-43); El Sauce (=El Sauz), 4000 ft., Victoria Mts. (MVZ 11,702-08); Guamuchil Rancho (CAS 46,809); La Burrera (SDSNH 45,062-64, 53,132-35); Arroyo Palmellar, 6 mi. ENE of Rancho La Burrera (LACM 34,592-93); "La Paz" (USNM 53,392); 40 mi. S of La Paz, 2 mi. above El Valle Perdido (CAS 90,544, 90,558); Miraflores (USNM 64,472); nr. km 70, Mex. Hwy. 1, 8 km SE of San Antonio (MCZ 136,188); San Bartolo (CAS 46,780-1, 46,783-86; UMMZ 56,044; MVZ 144,809-13); 1.1 mi. SE of San Bartolo (CAS 91,383); 1.5 mi. E of San Bartolo, ± 500 ft. (MVZ 73, 589); 3 mi. E of San Bartolo, ± 500 ft. (MVZ 73,570).

Sceloporus orcutti. *Holotype*: California: San Diego Co., Milquatay Valley, 2500-2600 ft. elevation (USNM 16,330). *Paratypes*: Same locality (USNM 16,238, -29, -33, -34). *Other specimens*: 15 mi. S of Canipole (LMK-SDSNH); 43 mi. N of Canipole (LMK-SDSNH); Rancho Chenque (SDSNH 51,044-46); Coyote Bay, 13 mi. SE of Mulegé (MVZ 37,318); 12 mi. E of El Arco (SDSNH 17,471); La Paz (LMK-SDSNH 38,339); 20.0 mi. W of La Paz, ± 500 ft. (MVZ 73,590); San Ignacio (MVZ 10,653, -54, -56, 13,597, -99; LMK-SDSNH 4,053, -54; UMMZ 76,482[2], 80,900); Misiòn Santa Gertrudis [Baja California Norte] (SDSNH 17,529-36).